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Phylogeny, Classification, and Biogeography of *Goniurosaurus kuroiwae* (Squamata: Eublepharidae) from the Ryukyu Archipelago, Japan, with Description of a New Subspecies

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ABSTRACT—The phylogenetic relationships of populations of *Goniurosaurus kuroiwae* from the Ryukyu Archipelago, Japan, are resolved using a cladistic analysis and their classification modified accordingly. The resultant phylogeny indicates that five subspecies should be recognized: *G. k. yamashinae* from Kumejima, *G. k. orientalis* from Tonakijima, Tokashikijima, Akajima, and Iejima, *G. k. kuroiwae* from Okinawajima, Sesokojima, and Kourijima, *G. k. toyamai* subsp. nov. from Iheyajima, and *G. k. splendens* from Tokunoshima. *Goniurosaurus k. yamashinae* is the sister taxon of the remainder. *Goniurosaurus k. kuroiwae* and *G. k. orientalis* are sister taxa which collectively form the sister group to the lineage composed of *G. k. toyamai* and *G. k. splendens*. *Goniurosaurus k. yamashinae* and *G. k. orientalis* are designated as metataxa because they are not demonstrably monophyletic or paraphyletic. A discriminant function analysis of the five subspecies shows *G. k. yamashinae* and *G. k. splendens* are separated from each other and from the other subspecies by a wide morphological gap. All these lineages were recognized as subspecies because this increases the phylogenetic content of the classification. The ancestor of the *G. kuroiwae* group may have dispersed into the Ryukyu Archipelago from continental China by way of a late Miocene to early Pliocene landbridge. The paleogeography of the Ryukyu Archipelago suggests that differentiation within *G. kuroiwae* resulted from the formation of the Ryukyu's contemporary configuration caused by rising Pleistocene sea levels.

INTRODUCTION

In a revision of the gecko family Eublepharidae, the genus Goniurosaurus was resurrected to contain the insular populations of eublepharids from the Gulf of Tonkin, China and the Ryukyu Archipelago, Japan [14, 15]. Thus, as it is currently constituted, *Goniurosaurus* contains at least two allopatric insular species; *G. lichtenfelderi* (Mocquard, 1897) [38] from the Island of Hainan and Iles de Norway in the Gulf of Tonkin, China [14] and *G. kuroiwae* (Namiye, 1912) [42] from 10 islands within the Ryukyu Archipelago, Japan [47]. There may also exist an undescribed species of *Goniurosaurus* from the Guizhou province of mainland China [33]. Grismer [15] revised the taxonomy of *G. kuroiwae* and recognized three subspecies; *G. k. yamashinae* (Okada, 1936) [44] of Kumejima Island, *G. k. kuroiwae* of Okinawajima Island and satellite islands to the west, and *G. k. splendens* (Nakamura *et* Uéno, 1959) [40] of Tokunoshima Island. Grismer's [15] classification resulted in the synonymy of *G. k. orientalis* (Maki, 1930) [35] with *G. k. kuroiwae* and placed the Kumejima Island population, considered at the time to be *G. k. orientalis* [41, 51], under the resurrected name of *G. k. yamashinae*. However, Grismer's [15] conclusions were provisional because he was only able to examine small series of specimens from Okinawajima and Tokunoshima Islands and relied on literature descriptions for some of the other insular populations.

In a more recent revision, Ota [47] referred all the insular populations west of Okinawajima Island (including that of Kumejima Island) to *G. k. orientalis*. The Okinawajima, Sesokojima, and Kourijima island populations remained under *G. k. kuroiwae* and the Tokunoshima population remained *G. k. splendens*. Both classifications [15, 47] suffer because they are based on overall similarity rather than derived similarity and not all insular populations were examined. In this paper we readdress the classification of *G. kuroiwae* from a phylogenetic standpoint based on a cladistic analysis of all known insular populations.

MATERIALS AND METHODS

Data were obtained from preserved (Appendix I) and living specimens. Grismer [15] demonstrated that *Goniurosaurus kuroiwae* is monophyletic based on its possession of the derived character states of tuberculate gular scales, unsheathed claws, and the absence of preanal pores. All specimens from the same island were treated as a single operational taxonomic unit and, as such, an *a priori* assumption of insular monophyly was adopted. Character states were polarized [34] based on the relationships suggested by Grismer [14–17] where *Goniurosaurus lichtenfelderi* served as the first outgroup and *Eublepharis, Hemitheconyx,* and *Holodactylus* as the second (Fig. 1).

Maddison *et al.* [34] stressed the importance of two sequentially aligned outgroups to ensure that polarity assignments are maximally parsimonious. It is likely, however, that the *Eublepharis-Hemitheconyx-Holodactylus* clade does not actually comprise the

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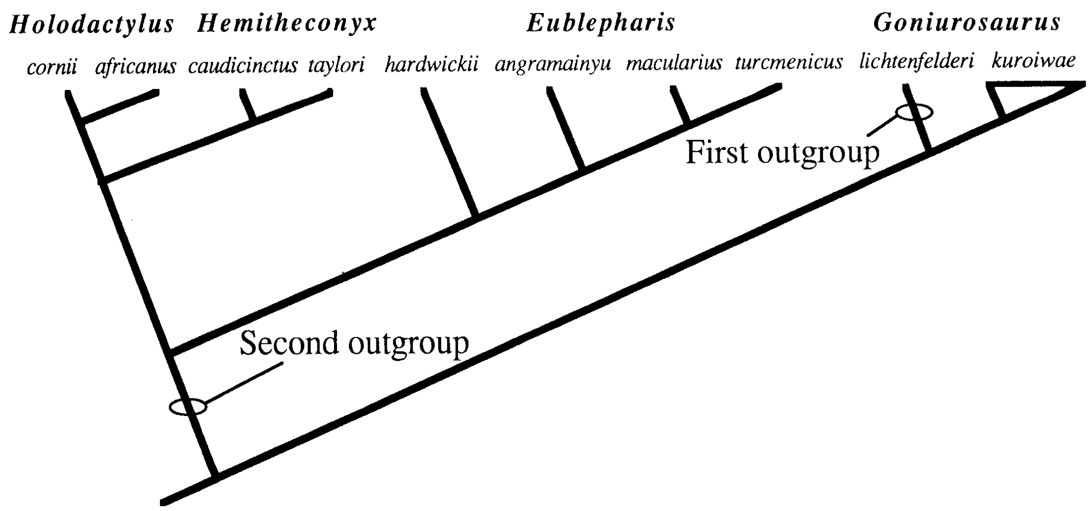

FIG. 1. Outgroup taxa and relationships of the first and second outgroups to *Goniurosaurus kuroiwae* after Grismer [14–17].

immediate second outgroup owing to the possible existence of an undescribed form of *Goniurosaurus* from mainland China [33]. This population is known from only a single specimen which was unavailable to us. Thus, the *Eublepharis-Hemitheconyx-Holodactylus* clade serves, at this point, as the best approximation of an immediate second outgroup. Because of a lack of homoplasy in the data set, computer algorithms were not necessary to aid in tree construction.

Following the cladistic analysis, scale counts from the Kumejima, Tokashikijima, Okinawajima, Iheyajima, and Tokunoshima populations were subjected to a multigroup discriminant function analysis (DA) with the MacIntosh version of BioΣtatII [50], in which each insular population was used as a predefined group. The sample sizes from the remaining islands (Table 1) were too small to yield statistically reliable results. Results from the DA were not used to construct phylogenetic relationships among the populations but only to aid in the morphological characterization and distinction of the terminal taxa suggested by the results of the cladistic analysis.

Terminology follows Grismer [15] and scale counts were taken as follows. *Supralabials*—the series posterior to the rostral and terminating with a scale at least twice the size of the surrounding granular scales. *Infralabials*—the series posterior to the mental and terminating with a scale at least twice the size of the surrounding granular scales. *Postmentals*—all scales except the first infralabials which contact the mental. *Preoculars*—the linear arrangement of granular scales between the anterior corner of the eye and the posterior margin of the external nares. *Eyelid fringe scales*—the lateralmost enlarged triangular scales encircling the eye. *Paravertebral tubercles*—the number of paravertebral tubercles between the limb insertions. *Midbody scales*—number of granular scales surrounding the body midway between limb insertions. *Fourth toe lamellae*—counting from the union of the third and fourth toes and terminating with the distal penultimate scale. *Scales surrounding claw on fourth toe*—all scales contacting the claw. The following counts were not used in the DA because of their incomplete representation in some or all of the populations. *Caudal scales*—the number of granular scales in the transverse caudal whorl of a non-regenerated tail at a point midway between the ankle and the knee when the hindlimb is adpressed against the tail. *Body bands*—number of transverse body bands between the nuchal loop and caudal constriction.

PHYLOGENETIC ANALYSIS OF CHARACTERS

1. *Dorsal tubercles*

In the Tokunoshima population, the dorsal body tubercles between the limb insertions are triangular to elliptical in cross-section and sharply keeled anteriorly. The tubercle keel is most pronounced dorsally, becoming less pronounced towards the base. Also, the degree of tubercle keeling increases posteriorly on the body with those tubercles between hind limb insertions being the most strongly keeled. Keeled tubercles do not occur on the head, nape of the neck, or tail. In the Kumejima population, the dorsal body tubercles are smooth and conical. In all other populations, tubercle-keeling only rarely occurs. When present, it is usually very weak and occurs only in a few tubercles between the hind limb insertions. In *Goniurosaurus lichtenfelderi, Eublepharis,* and *Holodactylus,* the tubercles are smooth and conical. Only in *Hemitheconyx* are the tubercles keeled. Therefore, the condition of sharply keeled tubercles in the Tokunoshima population is considered derived.

2. *Ventral scales*

The ventral scales of eublepharid geckos are usually hexagonal, flat, subimbricate to imbricate, and grade laterally into the granular scales of the dorsum. In the Tokunoshima population, the ventrals are juxtaposed and sharply raised, giving them a pointed or weakly tuberculate appearance. This condition is most evident in the pectoral region and fades posteriorly, grading into flat hexagonal imbricate interfemoral scales. Anteriorly, the pectoral scales grade into even more sharply pointed and raised gular scales. In all other populations of *Goniurosaurus kuroiwae,* as well as *G. lichtenfelderi, Eublepharis* and *Hemitheconyx,* the ventral scales are flat, wide, and subimbricate to imbricate. Anderson and Leviton [1] stated that the ventral scales of *E. angramainyu* are juxtaposed but we find them to be subimbricate. In *Holodactylus,* the ventral scales are juxtaposed but they are

TABLE 1. Meristic differences between the insular populations of *Goniurosaurus kuroiwae*. SL=supralabials; IL=infralabials; PM=postmentals; PO=preoculars; EF=eyelid fringe scales; TU=paravertbral tubercles; BO=midbody scales; 4T=fourth toe lamellae; CL=scales surrounding claw on fourth toe; CA=caudal scales; BB=body bands; I=incomplete; and A=absent.

Character	SL	IL	PM	PO	EF	TU	BO	4T	CL	CA	BB
yamashinae											
Kumejima (n=14)											
$\bar{x}$	8.0	8.4	4.6	21.0	53.6	28.8	148.6	18.4	6.0	47.7	4
range	7–9	7–9	4–5	19–23	44–65	21–33	132–156	17–20	6	43–53	4
SE	±0.2	±0.3	±0.2	±0.6	±2.3	±1.7	±2.7	±0.3	0	±2.9 (n=6)	0
orientalis											
Akajima (n=1)	9	10	5	22	63	35	144	19	6	48	4
Iejima (n=1)	9	8	5	22	63	29	145	20	6	50	4
Tokashikijima (n=50)											
$\bar{x}$	9.4	8.6	3.8	21.5	59.8	35.1	147.2	17.3	6.0	47.5	4 or I
range	8–11	7–11	3–5	17–24	53–66	31–40	135–159	16–19	5–7	42–52	
SE	±0.6	±0.2	±0.1	±0.3	±0.7	±0.5	±1.2	±0.2	±0.1	±1.2 (n=16)	
Tonakijima (n=2)											
$\bar{x}$	9	10	3.5	20.0	52.0	30.5	139.5	20.5	6	A	4
range	9	10	3–4	19–21	48–56	29–32	137–142	20–21	6	A	4
SE	0	0	±0.5	±1.0	±4.0	±1.5	±2.5	±0.5	0	A	0
kuroiwae											
Okinawajima (n=221)											
$\bar{x}$	9.4	8.7	5.0	21.4	60.2	33.4	150.9	17.1	6.0	49.8	A
range	7–11	7–11	4–6	19–23	54–70	29–43	139–162	15–20	6–7	40–57	A
SE	±0.2	±0.2	±0.1	±0.2	±0.7	±0.6	±1.3	±0.2	±0.1	±1.2 (n=124)	A
Kourijima (n=1)	9	9	4	23	51	34	140	15	6	51	A
Sesokojima (n=1)	8	8	5	21	57	31	137	17	6	A	A
toyamai											
Iheyajima (n=14)											
$\bar{x}$	9.3	8.3	4.6	21.4	55.6	37.2	149.8	17.3	5.9	47.5	3.8
range	8–10	7–10	3–5	20–23	53–59	34–42	140–158	16–20	5–6	40–53	3–4
SE	±0.2	±0.3	±0.2	±0.3	±0.5	±0.6	±1.9	±0.3	±0.3	±1.9 (n=6)	±0.1
splendens											
Tokunoshima (n=27)											
$\bar{x}$	9.0	8.6	2.9	20.5	54.1	20.0	132.4	16.2	7.4	50.4	3
range	8–10	7–10	2–4	18–24	46–59	22–29	121–146	15–18	6–9	46–61	3
SE	±0.1	±0.1	±0.1	±0.3	±0.5	±0.4	±1.4	±0.2	±0.2	±1.9 (n=8)	0

flat and not sharply raised. Therefore, juxtaposed and sharply raised ventrals in the Tokunoshima population is considered derived.

3. *Scales at base of digits*

In all *Goniurosaurus kuroiwae* except those from Kumejima Island, there are one to three (usually two) enlarged scales at the base of each digit on the hand and foot. These scales are two to three times the size of the scales of the adjacent palmar and plantar regions. This condition shows a slight indication of ontogenetic variation, being somewhat less pronounced in hatchlings and juveniles. In the Kumejima population, there is a single scale at the base of each digit which is occasionally slightly enlarged but rarely reaching twice the size of the surrounding scales. This is similar to the condition found only in the manus of *G. lichtenfelderi*. Enlarged scales at the base of the digits do not occur in *Eublepharis, Hemitheconyx,* and *Holodactylus*. Therefore, this condition in the manus of all populations of *G. kuroiwae,* except that from Kumejima Island, is considered derived.

4. *Lineate middorsal pattern*

Goniurosaurus kuroiwae from Akajima, Tokashikijima, Tonakijima, Iejima, Okinawajima, Kourijima, and Sesoko-

jima Islands have lineate tendencies in their dorsal banding patterns (Figs. 2 and 3). In the Akajima, Tokashikijima, Tonakijima, and Iejima populations, there is a middorsal stripe in the nape which usually extends far enough posteriorly to contact the first transverse body band near the forelimb insertions. Occasionally this stripe will continue far enough to contact the second transverse body band, nearly midway between the forelimb and hindlimb insertions, but rarely any

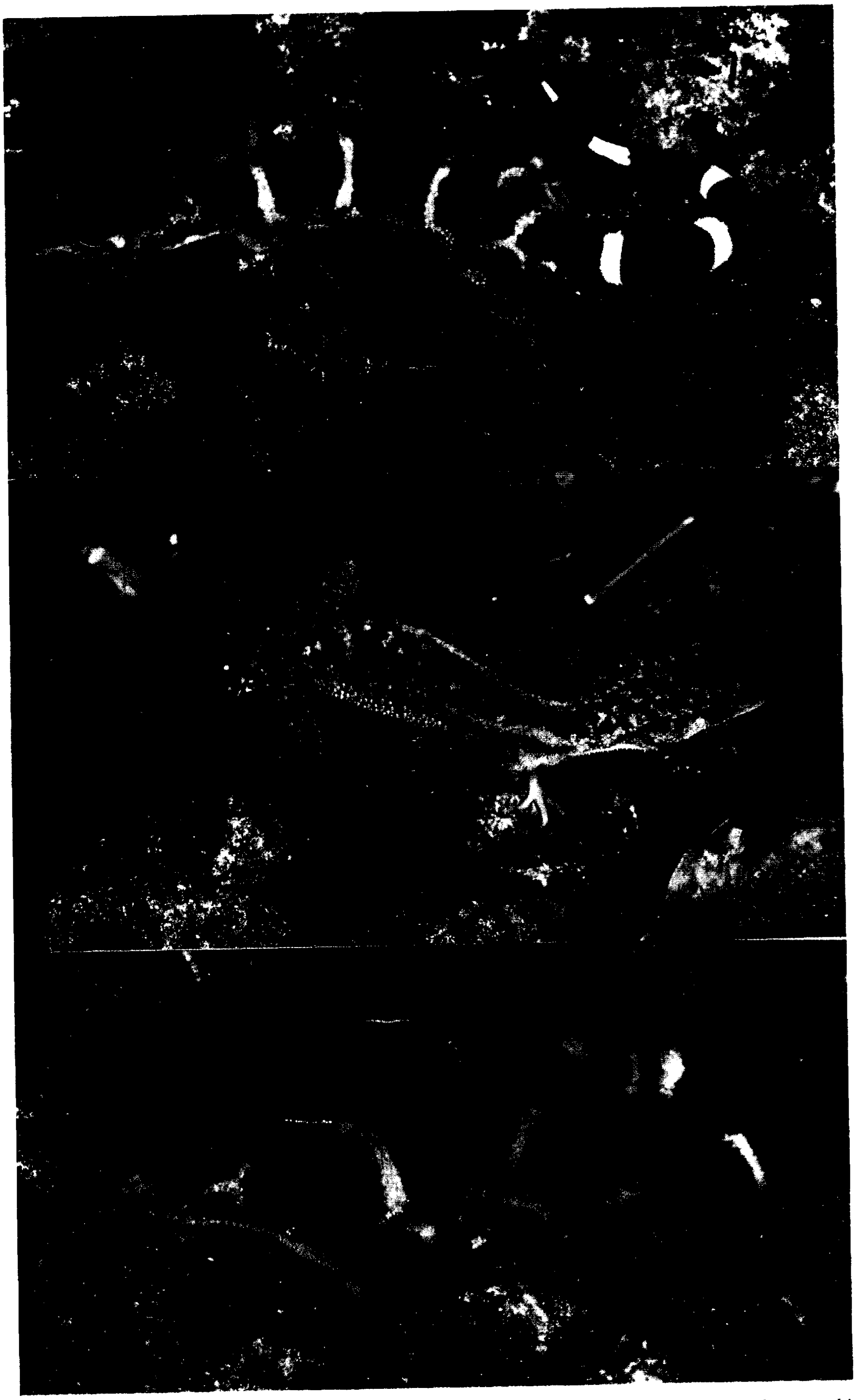

FIG. 2. Photographs of *Goniurosaurus kuroiwae* taken at the site of collection. Upper: juvenile *G. k. yamashinae* from Kumejima Island. Middle: *G. k. kuroiwae* from southern Okinawajima Island. Lower: adult *G. k. splendens* from Tokunoshima Island. Photographs by L. Lee Grismer.

FIG. 3. Photographs of *Goniurosaurus kuroiwae* taken at the site of collection. Upper: adult *G. k. toyamai* from Iheyajima Island. Middle: *G. k. orientalis* from Tokashikijima Island. Lower: juvenile *G. k. orientalis* from Akajima Island. Photographs by Masanao Toyama.

further except in the Okinawajima, Kourijima and Sesokojima populations. The Tonakijima population is known from one adult and one juvenile specimen. The adult (NSMT 02522: holotype of *G. k. orientalis*) has a middorsal stripe extending nearly one-half the way down the body. The juvenile (OPM 489) is banded and shows only weak evidence of striping on the nape of the neck. Middorsal lineation is most pronounced in the Okinawajima, Kourijima,

and Sesokojima populations where a stripe usually extends the entire length of the body and terminates at the caudal constriction (Fig. 2). On Okinawajima Island, there is some variation in that striping in the northernmost populations is not as well defined and a weak, faded banding pattern is sometimes present. Populations from the southern Okinawajima, however, have a bold, well-defined stripe and seldom show evidence of banding. In the remaining populations of *G. kuroiwae,* there is no evidence of middorsal striping (Figs. 2 and 3). In large specimens from Tokunoshima Island, there is occasionally a lack of dark pigmentation in the vertebral region that appears in preserved specimens to be a stripe. However, in living specimens this is merely a lightened area that develops with ontogeny. This region does not contain the same color pigments as the dorsal bands and as such does not constitute a middorsal stripe homologous with that described above. Such pigment loss in the vertebral region is common in large individuals of other eublepharids [18]. Tendencies toward dorsal pattern lineation do not occur in *G. lichtenfelderi*. Lineate tendencies are absent in *Eubelpharis hardwickii* but variable in *E. macularius, E. turcmenicus, E. angramainyu, Hemitheconyx caudicinctus,* and *Holodactylus*. Striping is absent in *Hemitheconyx taylori*. Therefore, the most parsimonious assumption is that lineate tendencies in the dorsal pattern of the Akajima, Tokashikijima, Tonakijima, Iejima, Okinawajima, Kourijima, and Sesokojima populations are derived.

5. *Banding pattern*

In all populations of *Goniurosaurus kuroiwae* except those from Okinawajima, Kourijima, and Sesokojima, there is a prominent dorsal pattern consisting of three to four transverse bands between the nape of the neck and the caudal constriction. Banding is bold and prominent in the Kumejima, Iheyajima, and Tokunoshima populations (Figs. 2 and 3). In the Akajima, Tokashikijima, Tonakijima, and Iejima populations, banding is prominent but the first band in the vicinity of the forelimb insertion may be incomplete (rarely absent). In the Okinawajima, Kourijima, and Sesokojima populations, banding is absent or incomplete. This condition is most obvious in populations from the southern portion of Okinawajima where there is usually no trace of banding (Fig. 2). In populations from northern Okinawajima Island as well as Kourijima and Sesokojima Islands, some specimens may retain some portions of the more posterior body bands. However, the bands are usually very irregular in shape and suffused with dark pigments from the surrounding ground color. This condition shows little or no ontogenetic variation. All outgroup taxa except *Holodactylus cornii* have a prominent banding pattern. Therefore, the incomplete to absent transverse dorsal banding pattern of the Okinawajima, Kourijima, and Sesokojima populations is considered derived.

6. *Hind limb banding*

In the Tokunoshima population, the posteriormost transverse body band extends laterally onto the dorsal surface of the thigh. In many specimens, the band runs parallel to the long axis of the hind limb uninterrupted to the knee. In others, it is interrupted medially and exists as a lineate blotch on the thigh and knee (Fig. 2). In all other populations of *Goniurosaurus kuroiwae,* the posteriormost body band does not extend along the long axis of the hind limbs. There may be light-colored elongate blotches on the dorsomedial surface of thigh of some specimens, but close examination reveals that they are oriented perpendicular rather than parallel to the long axis of the hind limb and in many cases, are discontinuous with the posteriormost transverse body band. In the outgroup taxa, the posteriormost transverse body band does not extend onto the hind limb. Therefore, the condition for the Tokunoshima population is considered derived.

7. *Interspace mottling*

The common condition in eublepharine geckos *sensu* Grismer [15] is for hatchlings to have dark, unicolored interspaces (or ground color) between the body bands, which become increasingly suffused and/or mottled with lighter coloration with age. This is the case in all *Goniurosaurus kuroiwae* except the Iheyajima and Tokunoshima populations where the adults retain unmottled dark interspaces (Figs. 2 and 3). Although the specimen of the Akajima population (OPM 341) is a juvenile, mottling in the interspaces is still observable (Fig. 3) and as with other eublepharines, assumed to be characteristic of adults. In the specimen from Iejima Island (KUZ 9991), the interspaces appear superficially like those in the Iheyajima and Tokunoshima populations. On close examination, however, it is clear that they are considerably lightened and not uniformly dark throughout. Adults of *G. lichtenfelderi* have both mottled and unicolored interspaces. The interspaces of adult *Eublepharis macularius, E. turcmenicus,* and *E. angramainyu* are mottled whereas those of *E. hardwickii* are unicolored. *Holodactylus* and *Hemitheconyx taylori* have mottled interspaces but they are generally unicolored in *Hemitheconyx caudicinctus*. Therefore, dark unicolored interspaces of the adults of the Iheyajima and Tokunoshima populations are considered derived.

8. *Juvenile coloration*

In all populations of *Goniurosaurus kuroiwae* except that of Kumejima Island, the color of the dorsal pattern (striped or banded) overlying the dark-brown ground color is always bright-orange to pink in hatchlings and juveniles. This color intensity usually remains into adulthood but sometimes fades into a cream-yellow hue (Figs. 2 and 3). The juvenile coloration of the dorsal pattern in specimens from the Kumejima population is whitish. The dorsal color pattern in the juveniles of both outgroups consists of yellow to whitish hues and is never bright-orange to pink at any stage of life. Therefore, the latter condition is considered derived for all populations of *G. kuroiwae* except that of Kumejima Island.

9. *Eye color*

The color of the iris in all *Goniurosaurus kuroiwae* except the Kumejima population is blood-red (Figs. 2 and 3). In the Kumejima population, *G. lichtenfelderi,* and *Eublepharis* (*E. hardwickii* and *E. angramainyu* not available for examination), the iris is yellow-brown to gold in color. In *Hemitheconyx caudicinctus* and *Holodactylus africanus,* the iris is usually a very dark brown. Living *Hemitheconyx taylori* and *Holodactylus cornii* were unavailable for examination. Therefore, based on the relationships of the outgroup taxa observed (Fig. 1), a blood-red iris is considered to be derived for the ingroup. If, however, a blood-red iris is present in the outgroup taxa that were not examined, the polarity assignment would be equivocal.

10. *Body stature*

The overall body stature in the Iheyajima population is robust, whereas that in the other populations of *G. kuroiwae,* as well as *G. lichtenfelderi,* more slender (Fig. 4). Thus, although the state of this character is not defined in the members of the second outgroup due to their much divergent body proportion, the robust body stature in the Iheyajima population is considered derived within the genus *Goniurosaurus* by assuming the Kumejima population as a first functional outgroup and *G. lichtenfelderi* as a second outgroup [60] (see below).

RESULTS

There is only one single most parsimonious tree which has a consistency index value of 1.0 (Fig. 5). The distribution of the derived character states (Table 2) suggests that the Kumejima population is the sister taxon of the remaining nine insular populations of *Goniurosaurus kuroiwae* (Fig. 5). Ota [47] placed the Kumejima population (*G. k. yamashinae: sensu* Grismer [15]) in *G. k. orientalis*. However, it is apparent here that such a classification would result in the demonstrative paraphyly of the latter (Fig. 5). Although the Kumejima population is discretely diagnosable from all other *G. kuroiwae*, it lacks character state support for its monophy-

TABLE 2. Distribution of derived (1) and primitive (0) character states among the island populations of *Goniurosaurus kuroiwae* and the outgroup taxa. ?=Character was not examined because live animals were not available to us. — =Character state was not defined due to the great divergence in related body portions.

Characters	1	2	3	4	5	6	7	8	9	10
Taxa										
Ingroup										
G. k. yamashinae										
Kumejima	0	0	0	0	0	0	0	0	0	0
G. k. orientalis										
Akajima	0	0	1	1	0	0	0	1	1	0
Tonakishima	0	0	1	1	0	0	0	1	1	0
Tokashikijima	0	0	1	1	0	0	0	1	1	0
Iejima	0	0	1	1	0	0	0	1	1	0
G. k. kuroiwae										
Okinawajima	0	0	1	1	1	0	0	1	1	0
Kourijima	0	0	1	1	1	0	0	1	1	0
Sesokojima	0	0	1	1	1	0	0	1	1	0
G. k. toyamai										
Iheyajima	0	0	1	0	0	0	1	1	1	1
G. k. splendens										
Tokunoshima	1	1	1	0	0	1	1	1	1	0
Outgroups										
G. lichtenfelderi lichtenfelderi	0	0	0	0	0	0	0,1	0	0	0
G. l. hainanensis	0	0	0	0	0	0	0,1	0	0	0
Eublepharis hardwickii	0	0	0	0	0	0	1	0	?	—
E. angramanyu	0	0	0	0,1	0	0	0	0	?	—
E. turcmenicus	0	0	0	0,1	0	0	0	0	0	—
E. macularius	0	0	0	0,1	0	0	0	0	0	—
Holodactylus africanus	—	0	0	0,1	0	0	0	0	0	—
H. cornii	0	0	0	0,1	0	0	0	0	?	—
Hemitheconyx caudicinctus	1	0	0	0,1	0	0	1	0	0	—
H. taylori	1	0	0	0	1	0	0	0	?	—

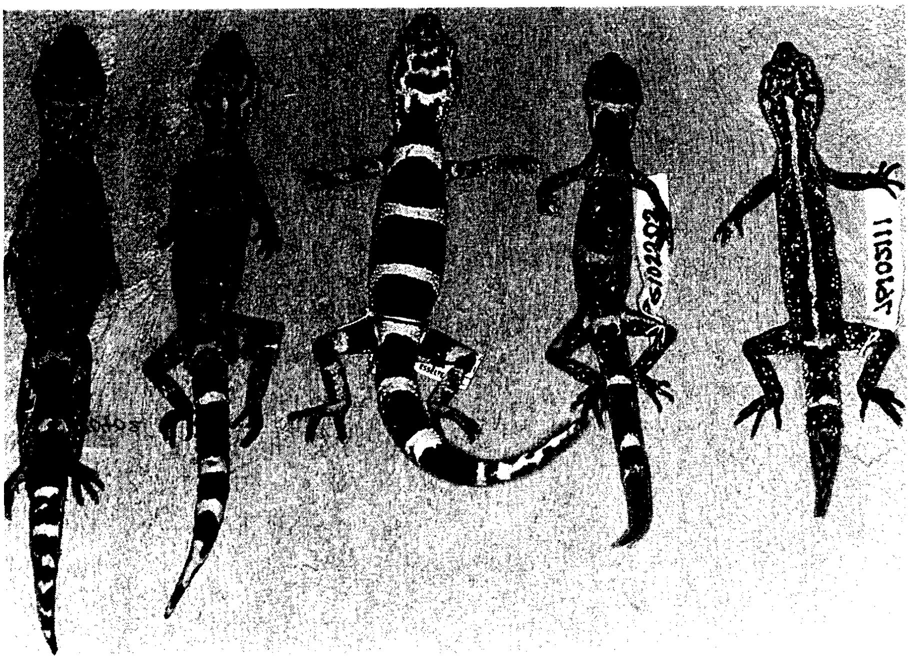

FIG. 4. Body stature of the five subspecies of *Goniurosaurus kuroiwae*. From left to right *G. k. yamashinae*, TPN 78050402 (SVL=87.5) from Kumejima Island; *G. k. orientalis*, TPN 78052101 (SVL=83.8) from Tokashikijima Island; *G. k. toyamai*, KUZ 9983 (SVL=84.6) from Iheyajima Island; *G. k. splendens*, TPN 76102202 (SVL=77.2) from Tokunoshima Island; and *G. k. kuroiwae* TPN 76102111 (SVL=79.9) from Okinawajima Island.

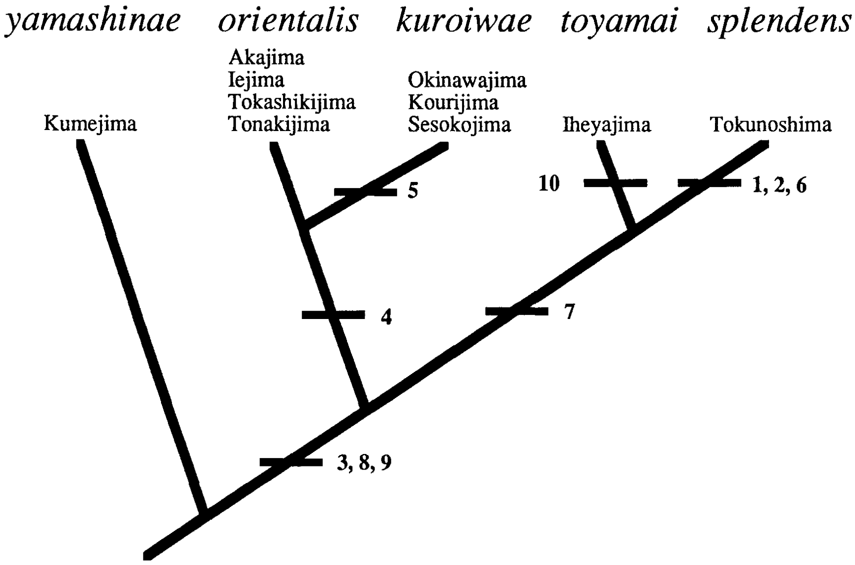

FIG. 5. Cladistic relationships of the insular populations of *Goniurosaurus kuroiwae* and the resultant classification. Numbered horizontal bars represent the presence of the following derived character states: 1=tubercles sharply keeled; 2=ventrals juxtaposed; 3=enlarged scale(s) at base of digits; 4=lineate tendencies in middorsal pattern; 5=dorsal banding absent; 6=posteriormost body band extending onto hind limb; 7=interspace mottling absent; 8=orange-pink dorsal pattern in juveniles; 9=iris red; 10=body robust.

ly or demonstrable paraphyly, and thus, is given a metataxon designation [12] and recognized here as *G. k. yamashinae* (see [6, 8, 10, 25] for differing viewpoints on usage of this designation). The DA shows that *G. k. yamashinae* is well isolated from all other populations examined along the second axis except for a very slight degree of overlap with that of Okinawajima (Fig. 6). Standardized canonical coefficients for the first two variates presented in Table 3 account for 92.26% of the observed variation.

The remaining nine insular populations form a well-corroborated monophyletic group diagnosed by the derived character states of an enlarged scale at the base of each digit, a blood-red iris, and a bright orange to pink hatchling and juvenile color pattern (Fig. 5). Within this clade, there are two major monophyletic lineages. The first lineage consists of the Okinawajima, Kourijima, Sesokojima, Tonakijima, Tokashikijima, Iejima, and Akajima populations. This group is diagnosed by the derived acquisition of lineate

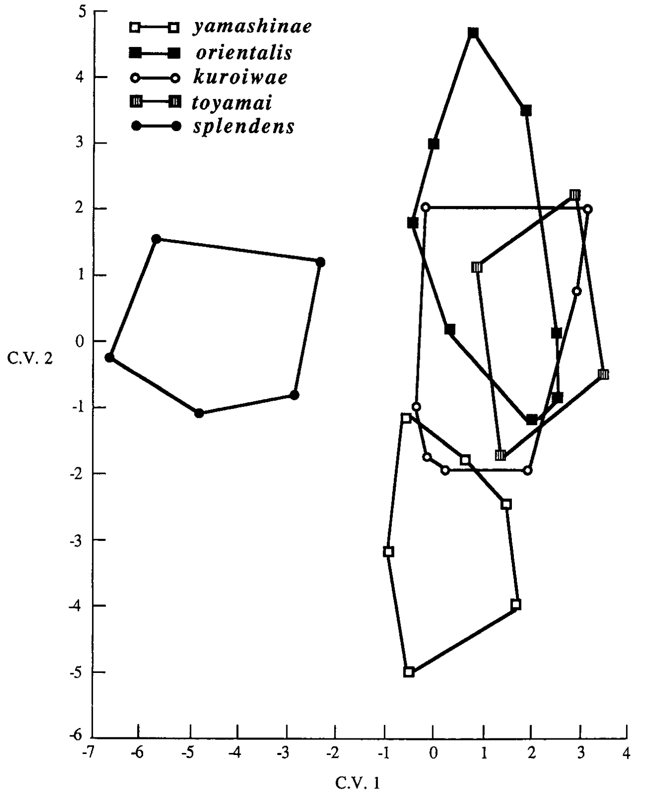

FIG. 6. First two canonical variates of the DA (C.V.1=78.78% and C.V.2=13.48% of the total variation). *Goniurosaurus kuroiwae splendens* from Tokunoshima Island (n=27); *G. k. kuroiwae* from Okinawajima Island (n=221); *G. k. orientalis* from Tokashikijima Island (n=50); *G. k. yamashinae* from Kumejima Island (n=14), *G. k. toyamai* from Iheyajima Island (n=14). Polygons were constructed by connecting the most peripherally located points of each plot.

TABLE 3. Standardized canonical coefficients for the first two variates (C.V.1 and C.V.2) from the multigroup discriminant function analysis (DA) of the nine characters from the Kumejima, Tokashikijima, Okinawajima, Iheyajima, and Tokunoshima populations. Symbols follow those of Table 1.

Character	C.V.1	C.V.2
SL	−0.10	0.70
IL	−0.01	0.05
PM	0.70	−0.78
PO	0.02	0.11
EF	0.05	0.16
TU	0.29	0.15
BO	0.03	−0.02
4T	0.25	−0.38
CL	−0.92	0.31

tendencies in the dorsal pattern (Fig. 5). Within this group there are two recognizable subgroups. The first is a monophyletic lineage containing the Okinawajima, Kourijima, and Sesokojima populations which is diagnosed by the derived acquisition of a dorsal pattern consisting of bands that are incomplete to absent. This group was previously referred to as *Goniurosaurus kuroiwae kuroiwae* [15 (in part), 41, 47] and its monophyly supports its continued recognition. The DA shows that *G. k. kuroiwae* is nearly completely separated from *G. k. yamashinae* along the second axis and completely separated from the Tokunoshima population along the first axis (Fig. 6). However, it greatly overlaps the Tokashikijima and Iheyajima populations along both axes (Fig. 6).

The second subgroup within this lineage is composed of the Tonakijima, Tokashikijima, Iejima, and Akajima (see below) populations (Fig. 5). Although this group is not demonstrably monophyletic or paraphyletic, it is diagnosable from *Goniurosaurus kuroiwae kuroiwae* as well as all the other populations (Fig. 5). Because Tonakijima Island is the type locality of *G. k. orientalis* [35], that name has priority for this group and it is given a metataxon designation (*G. k. orientalis*). The DA shows that *G. k. orientalis* is completely separated from *G. k. yamashinae* along the second axis and from the Tokunoshima population along the first axis but that it greatly overlaps the Okinawajima and Iheyajima populations along both axes (Fig. 6).

The second major monophyletic lineage also comprises two subgroups and is diagnosed by its derived lack of interspace mottling (Fig. 5). The first subgroup is a monophyletic lineage composed of the Tokunoshima population and diagnosed by the derived acquisition of keeled dorsal tubercles, juxtaposed and sharply raised ventral scales, and the posteriormost transverse body hand extending onto the hind limbs. This population was first described as *Eublepharis splendens* by Nakamura and Uéno [40], and has subsequently been recognized as *Goniurosaurus kuroiwae splendens* [15, 41, 47, 51]. The evidence presented here for its monophyly supports its continued recognition. The DA shows that *G. k. splendens* is well separated from *G. k. yamashinae* along the second axis and from all other populations along the first axis (Fig. 6).

The second subgroup of this lineage is composed of the Iheyajima population (Fig. 5). This population was placed within *G. k. orientalis* (*sensu* Ota [47]) based on its overall similarity in color pattern and scale meristics to the populations of Tonakijima, Tokashikijima, Iejima, and Akajima [47, 52, 56]. It is shown here, however, that the Iheyajima population differs from *G. k. orientalis* in that it lacks the derived state of lineate tendencies in the dorsal banding pattern that unite *G. k. orientalis* with *G. k. kuroiwae*. Furthermore, it has the derived state of a lack of interspace mottling which groups it with G. k. *splendens*. Thus, continued placement of this population in *G. k. orientalis* would make the latter demonstrably paraphyletic. Additionally, it is well-separated from *G. k. splendens* by its lacking the derived character states of keeled dorsal tubercles, juxtaposed and sharply raised ventral scales, and posteriormost body band extending onto the hind limbs. The DA shows that it is completely separated from *G. k. yamashinae,* along the second axis and from *G. k. splendens* along the first axis but greatly overlaps *G. k. orientalis* and *G. k. kuroiwae* along

both axes (Fig. 6).

It is clear that the Iheyajima population forms a separate monophyletic lineage differing from *splendens* by its lack of the derived states of characters 1, 2, and 6, and the possession of derived state in character 10. Additionally, its continued recognition as *Goniurosaurus kuroiwae orientalis* would result in the demonstrative paraphyly of the latter. Thus, separate subspecific recognition is warranted and we consider this population to be:

Goniurosaurus kuroiwae toyamai subsp. nov.
(Fig. 7)

Suggested English name: Iheyajima Leopard Gecko
Suggested Japanese name: Iheya-Tokagemodoki
Eublepharis kuroiwae orientalis: Toyama, 1984, p. 270 [56] (part).
Goniurosaurus kuroiwae orientalis: Ota, 1989, p. 230 [47] (part).

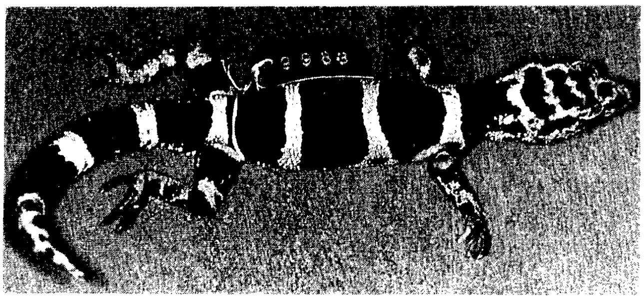

Fig. 7. Holotype of *Goniurosaurus kuroiwae toyamai* KUZ 9983 from Iheyajima Island, Okinawa Prefecture, Japan.

Holotype. KUZ 9983, collected by S. Tanaka on Iheyajima Island, Okinawa Prefecture, Japan, on 4 July 1977.

Paratypes. Thirteen paratypes from the same locality as the holotype: KUZ 9978–9982, 9985–9988; TPN 77032201, 77070301, 7707401–7707402.

Diagnosis. *Goniurosaurus kuroiwae toyamai* differs from all other subspecies of *G. kuroiwae* in its overall robust body stature and greater mean number of paravertebral tubercles (37.2 : 34–42). It differs further from *G. k. yamashinae*, *G. k. orientalis*, and *G. k. kuroiwae* in that adults lack interspace mottling; from *G. k. orientalis* and *G. k. kuroiwae* in lacking lineate tendencies in its dorsal pattern and having a lower mean number of eyelid fringe scales (55.6 : 53–59); from *G. k. orientalis* by having a slightly higher mean number of postmental scales (4.6 : 3–5); from *G. k. kuroiwae* in having a complete dorsal banding pattern; from *G. k. yamashinae* by having enlarged scales at the base of its digits, orange-pink juvenile color pattern, blood-red iris, a higher mean number of supralabial scales (9.3 : 8–10), and a lower mean number of fourth toe lamellae (17.3 : 16–20); and from *G. k. splendens* by lacking sharply keeled dorsal tubercles, juxtaposed and sharply raised ventral scales, the lateral extension of the posteriormost body bar onto the hind limb, and by having a greater mean number of postmental scales (4.6 : 3–5), midbody scales (149.8 : 140–158), fourth toe lamellae (17.3 : 16–20), and a lower mean number of scales surrounding the claw on the fourth toe (5.9 : 5–6).

Distribution. *Goniurosaurus kuroiwae toyamai* is known only from Iheyajima Island of the Okinawa Group, Ryukyu Archipelago, Japan (Fig. 8).

Description of holotype. Adult male; SVL 83.8 mm; head triangular, wider than neck, covered with uniform granular scales interspersed with enlarged tubercles increasing in size posteriorly; tubercles absent from rostrum, group of enlarged tubercles immediately anterior to orbit; rostral convex and rectangular, twice as wide as high, middorsal portion partially sutured dorsomedially, bordered laterally by first supralabial and prenasal, dorsolaterally by supraprenasal on left and intercalary scale on right, and dorsally by four enlarged granular scales; external nares subelliptical with

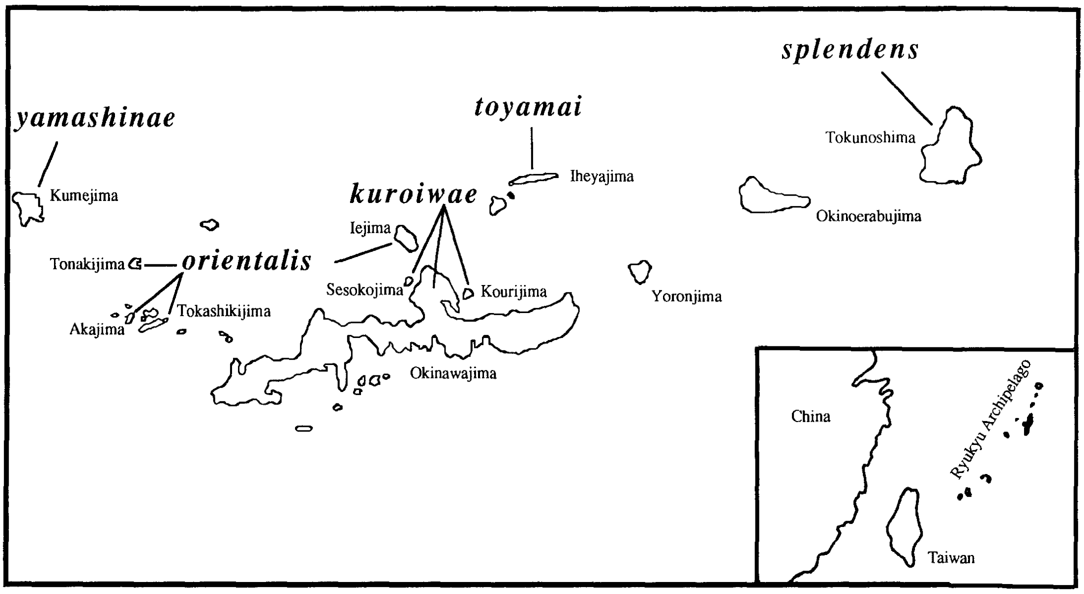

Fig. 8. Distribution of the subspecies of *Goniurosaurus kuroiwae* in the Ryukyu Archipelago, Japan.

long axis sloping forward, bordered anteriorly by prenasal and supraprenasal, dorsally and posteriorly by 8(R)-7(L) granular scales, and ventrally by one (R and L) granular scale and prenasals; prenasals with long recurved ventral portion; supraprenasal square, separated medially by four granular scales; supralabials 9(R)-10(L), first two of series square, the remaining rectangular, decreasing in size posteriorly, grading into granular scales along ventral margin of posterior section of upper jaw, posteriormost raised centrally; rostral granules equal in size; preoculars 21(R)-20(L); eyes relatively large, pupils vertical and with convex slightly serrate margins (visible in life); eyelid fringe scales 59 (R and L), triangular, those of upper eyelid slightly enlarged and conical; outer surface of upper eyelid consisting of small uniform granular scales equal in size to those on top of head, base of upper eyelid bordered by row of enlarged tuberculate scales; 63 scales across top of head between posterior corners of eyes; a fold of skin consisting of granular scales originating in suborbital region extends posteroventrally across angle of jaw; external auditory meatus elliptical with long axis directed dorsoventrally, single elongate tubercle bordering anterior margin; tympanum deeply recessed; mental triangular acutely tapering but rounded at posterior tip, bordered laterally by first infralabials and posteriorly by four slightly enlarged postmentals; 10(R)-9(L) infralabials, anteriormost square grading posteriorly into smaller rectangularly shaped infralabials that grade posteriorly into granular scales bordering dorsal margin of upper jaw; ventral margin of posteriormost infralabials well elevated from surrounding gulars; gular region covered with juxtaposed conical scales interspersed with enlarged tubercles; 56 rows of gulars between postmentals and an imaginary line between posterior margins of auditory meati; gulars grading posteriorly into flat hexagonal subimbricate pectoral scales and larger hexagonal imbricate ventral and interfemoral scales.

Neck narrower than body, covered with uniform granular scales, interspersed with several large sharply pointed conical tubercles on nape; tubercles on body conical and prominent, long axes directed posteriorly; body tubercles numerous, distributed evenly on dorsum and increasing in size posteriorly from nape of neck to caudal constriction, grading into distinct repeating caudal whorls; tubercles at caudal constriction twice the size of those on nape, tubercles surrounded by 9–12 granular scales; 36 paravertebral tubercles between limb insertions, strict vertebral row absent.

Limbs robust, covered with uniform granular scales interspersed with tubercles roughly one-half the size of those on body; granular scales grading distally into slightly flattened, weakly subimbricate scales of dorsal surface of manus and pes; 43(R)-45(L) granular scales around humeral region and 39(R)-38(L) around forearm; hindlimbs roughly twice as thick as forelimbs, covered with uniform granular scales interspersed with enlarged tubercles, those of posterofemoral region equal in size to those on body; 51(R)-53(L) granular scales around femoral region and 47(R)-48(L) around forelegs; pes covered ventrally with juxtaposed scales, those at heel enlarged; 1–2 enlarged scale(s) at base of each digit; subdigital lamellae narrow, nearly equal in size to slightly smaller lateral digital scales; 18(R)-17(L) subdigital lamellae on fourth toe; digits conical, increasing in length from first to fourth, fifth shorter than fourth.

Body robust, covered with granular scales grading ventrally into flattened, subimbricate ventral scales; 141 granular scales around midbody; ventral interfemoral scales large, flat, imbricate, grading posteriorly into small granular scales anterior to vent; region immediately posterior to vent covered with large flat imbricate scales, greatly swollen, with two upward-curving bony spurs arising from lateral margins.

Tail conical, thickest at base, covered with small rectangular imbricate scales arranged in transverse caudal whorls and repeated series of greatly enlarged and sharply pointed tubercles occurring in caudal whorls; caudal tubercles absent ventrally and decreasing in size laterally and posteriorly; ventral caudals larger and more nearly square than dorsal caudals; posterior one-quarter of tail regenerated and covered with slightly raised granular scales.

Coloration in life. Ground color of dorsum (including limbs and tail) uniform dark brown; top of head mottled in dark brown and cream; wide dark brown pre- and postorbital stripes; eyelid fringe scales cream-colored giving slight appearance of eye-ring; labial region light-brown to cream-colored; four wide, immaculate, transverse, cream-colored body bands between nape of neck and caudal constriction; bands blend ventrolaterally into light-colored ventrum; back of head bordered by incomplete nuchal band; forelimbs with large cream-colored symmetrical blotches in brachium, elbow, and antebrachium; hind limbs with large cream-colored symmetrical blotches in groin, knee, and dorsoposterior crus regions; two bands on original portion of tail suffused with reticulate pattern of dark-brown ground color; ventral surface of head, limbs, and body, immaculate light-brown; iris blood-red.

Variation. Paratypes closely approximate the holotype in morphology, meristics, and coloration. The most significant variation occurs in banding pattern and coloration. In three specimens (KUZ 9981–82, 9988), the third transverse body band is incomplete and interrupted medially. Three other (KUZ 9986–87; TPN 77070301) have three instead of four bands between the nuchal band and caudal constriction. All other populations of *Goniurosaurus kuroiwae* have four bands except its sister taxon *G. k. splendens*, which always has three. The coloration of the bands in hatchling and juvenile *G. k. toyamai* is bright orange-pink. This coloration may fade to a yellowish to cream-colored banding pattern in adulthood, although some adults maintain the juvenile coloration to some extent. Regenerated tails lack all aspects of banding observed in original tails. Regenerated tails are mostly dark-brown like the body ground color but become overlain with a reticulum of uneven light-purple uneven blotches.

Etymology. This poulation is named in honor of Mr. Masanao Toyama in recognition of his vast number of

contributions to the herpetology of the Ryukyu Archipelago including the first distributional record of *Goniurosaurus kuroiwae* from Iheyajima Island [56].

DISCUSSION

Phylogeny and similarity

The classification of *Goniurosaurus kuroiwae* presented here does not differ greatly from those of Grismer [15] and Ota [47]. It differs from Grismer [15] only in that it considers the populations of Tonakijima and Tokashikijima Islands to be *G. k. orientalis* rather than *G. k. kuroiwae*. It differs from Ota [47] in that the population from Kumejima Island is considered to be *G. k. yamashinae* rather than *G. k. orientalis*, and that the population from Iheyajima Island is considered to be a distinct subspecies *G. k. toyamai*, rather than *G. k. orientalis*.

Owing to the diagnosability of *Goniurosaurus kuroiwae yamashinae* (Figs. 5 and 6), it is clearly a lineage in the sense of Frost and Hillis [10]; that is, it is a sexual plexus viewed through time. We are less convinced, however, about the lineage status of *G. k. orientalis* primarily because of the inclusion of the Iejima population and the distance of that island from Tonakijima, Tokashikijima, and Akajima Islands (Figs. 8 and 9). The latter three islands are in close geographic proximity and situated within a cluster of islands approximately 35 km west of the southwestern tip of Okinawajima between it and Kumejima Island (Fig. 8). Iejima Island on the other hand, lies only 15 km off the western tip of the Motobu Peninsula of Okinawajima. Populations of *G. kuroiwae* from Kourijima and Sesokojima Islands, which are also geologically associated with the Motobu Peninsula, are not distinguishable from those of Okinawajima and are considered to be *G. k. kuroiwae*. The placement of the Iejima Island population in *G. k. orientalis* is based on the complete dorsal banding pattern of the single known specimen. More specimens from this island would certainly help to clarify its relationships but unfortunately this population may be greatly reduced or extinct due to habitat alteration.

The DA demonstrates the great morphological similarity among *Goniurosaurus kuroiwae orientalis, G. k. kuroiwae*, and *G. k. toyamai*. If we were to construct our classification based on the phenetic relationships of the DA, we would recognize *G. k. yamashinae* and *G. k. splendens* but would consider *G. k. orientalis, G. k. toyamai*, and *G. k. kuroiwae* to all be *G. k. kuroiwae*. However, it is probable that the apparent meristic similarity among the Tokashikijima, Okinawajima, and Iheyajima populations has resulted from independent microevolution in these allopatric populations. Therefore, we prefer to base our classification on the hypothesis of phylogenetic relationships. We believe this results in a more meaningful classification because it is based on common ancestry rather than overall similarity, and thus reflects similarities due to the evolution of shared novelties rather than parallel evolution.

Species vs. subspecies

There recently has been renewed controversy over the use of the subspecies category [2–5, 9–11, 19, 20, 30, 39, 53, 58] as it specifically pertains to herpetology. We believe this issue can be broken down into two general themes. The first concerns the ontology of species and determining wether or not a population represents an individual that should be named and if so, at what taxonomic level. The second is a more general issue concerning the types of information to be retrieved from classifications.

In regard to the second question, phylogenetic systematists want a classification that is consistent with recoverable phylogenetic history [10]. Therefore, they are opposed to classifications that recognize demonstrably paraphyletic taxa including subspecific entities that subjectively divide up various sections of a continuous populational cline. Evolutionary systematists prefer classifications that represent the historical extent of phenetic divergence [36]. Thus, they are willing to recognize demonstrably paraphyletic taxa and consider them one of the consequences of evolution. Therefore, dividing up a continuously breeding population into definable subspecies is acceptable because this may represent the early stages of evolutionary divergence.

Neither system is right or wrong, they are just different. And each is attempting to construct a classification from which different types of information can be extracted. What needs to be decided is which kind of information has more utility to science in general. It is our opinion that a phylogenetic classification has a broader utility because it forms the phylogenetic foundation upon which both systematic and non-systematic evolutionary biologists can formulate hypotheses as to how and why character states and other biological systems have evolved [e.g., 43, 55, 59]. This does not mean that we are advocating abandoning the subspecies concept, however. In fact, at this point in time, we believe that the subspecies categoly may be able in some situations, to provide a classification with additional phylogenetic information. However, the advantages and disadvantages of each situation need to be carefully evaluated on a case by case basis. We do believe that demonstrably paraphyletic taxa should not be used in a classification because they obscure more information than they reveal as well as misrepresent history.

In regard to the first question, the subspecies category was originally intended to be used for populations of geographic variants of continously interbreeding populations [37, 62] and has subsequently enjoyed a broad use of this type of pattern class designation. The problem, however, is that this type of category in a classification, is often inconsistent with the recoverable phylogenetic history. Because these categorical assignments are not lineage (historically) based, they usually do not represent individuals (*sensu* [13, 21, 22]) but classes, and can actually distort history. Additionally, such categories often offer little information because the populations being recognized are usually only weakly diagnosable. It recently has been argued, that if adjacent

populations are interbreeding with one another (e.g. they are not on separate phylogenetic trajectories) they cannot be considered independent evolutionary units [10, 26]. And in such situations, a phylogenetic classification would argue for a single taxon. This criterion is often correct and will go a long way in resolving problems surrounding pattern class taxonomy but it is far too broad. Because of the degrees of differences between varying zones of contact between many diagnosable entities, some of these entities may not be pattern classes or simple geographic variants. They may actually be monophyletic lineages undergoing secondary contact in which case their lineage identity should be retained. Because phylogenetic systematics is a retrodictive discipline and not a predictive discipline, there is no way of knowing from just a slice of time (the present) whether or not these populations will subsume one another. Therefore, it is more conservative to base our decisions on what can be inferred from the past. Before any type of an "all or nothing" criterion can be convincingly argued (or if it can be argued at all) concerning the importance of reproductive compatibility in contact zones, many more case studies will need to be examined. We believe that there may very well be discretely diagnosable widely distributed populations (lineages) that narrowly intergrade on the fringes of their ranges with other such adjacent populations and that this intergradation does not preclude them from being on separate phylogenetic trajectories.

By abandoning the traditional concept of what a subspecies is supposed to represent (geographic variants or pattern classes) and applying the criteria of historical individuality (*sensu* Kluge [26]) to these smallest evolving lineages, the phylogenetic content of classifications may be augmented. This situation is actually less problematic when dealing with allopatric populations and *Goniurosaurus* is a good example with which to work. The evolutionary species concept (*sensu* Frost and Hillis [10]) would recognize all the different taxa of *Goniurosaurus* as distinct species because each is diagnosable and allopatric with respect to one another. This is true, and it clearly indicates that these taxa are on their own separate phylogenetic trajectories. However, this classification would provide less recoverable phylogenetic information (Fig. 10). All that would exist is a list of seven species of *Goniurosaurus* with no indication of how any of them are related. However, if these taxa are considered as subspecies of *G. kuroiwae* and *G. lichtenfelderi*, then more phylogenetic knowledge is imparted into the classification (Fig. 11). In other words, we know that there are at least two monophyletic lineages within *Goniurosaurus* and that within each of those lineages, there has been additional evolution. And if we want our classifications to be information retrieval systems consistent with recoverable phylogenetic history [10], then this system is clearly providing more information.

All the populations of *Goniurosaurus* could be considered as species and the classification indented accordingly [61] which would provide the same amount of information. However, this classification only would be useful when it is at hand for referral. For example, if a paper was written describing various physiological differences between the insular popoulations of *Goniurosaurus* under an indented phylogenetic classification system with no subspecies, we would not know how the taxa were related or the evolutionary implications of the results simply by reading the paper. If, however, the subspecific classification proposed above was used, an evolutionary interpretation of the data becomes more readily apparent because we are able to infer something about relationships from the nomenclature. Now obviously,

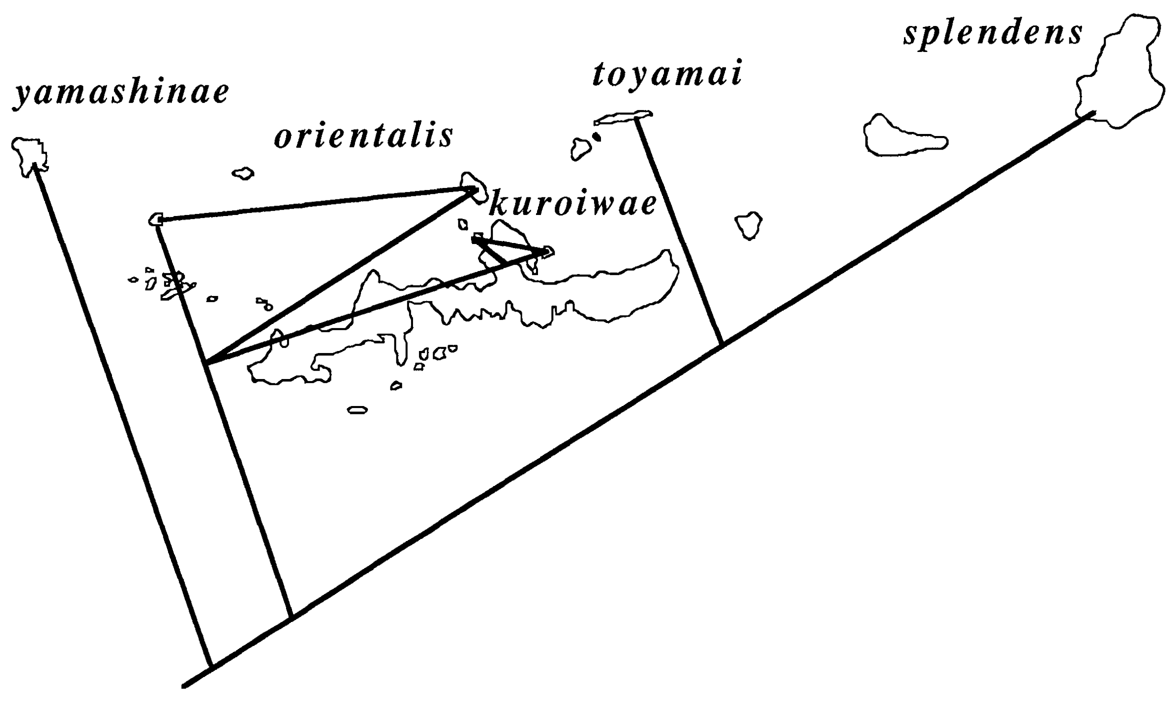

FIG. 9. Area cladogram of the subspecies of *Goniurosaurus kuroiwae*.

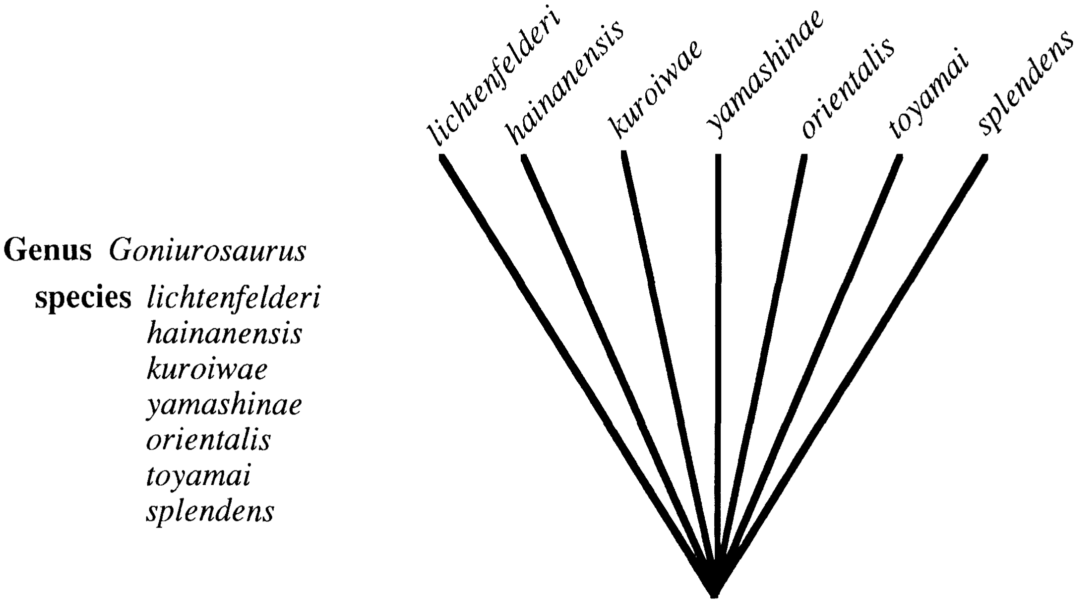

FIG. 10. Classification of *Goniurosaurus* on the left recognizing all populations as species and the amount of recoverable phylogenetic information from that classification on the right.

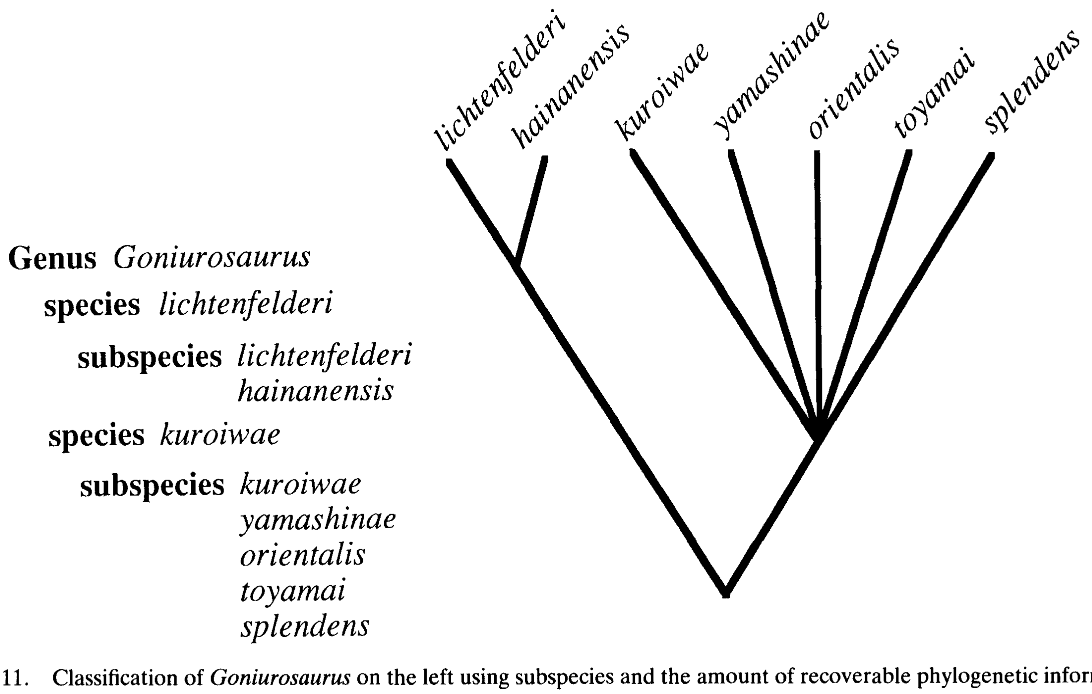

FIG. 11. Classification of *Goniurosaurus* on the left using subspecies and the amount of recoverable phylogenetic information from that classification on the right.

this information could be obtained by reviewing the original phylogeny but unfortunately this is far too often neglected by non-systematic evolutionary biologists (see Dial and Grismer [7]).

The disadvantage in recognizing these taxa as subspecies lies primarily in the original connotation of the subspecies category: that of intergrading geographic variants or pattern classes, which is something these populations are not. In fact, it is the historical inertia of this connotation that is the major disadvantage to considering the name "subspecies" to replace the name Kluge [26] uses for lineage individuality ("species"). However, we believe at this point it is still best to emphasize the phylogeny of this group by way of its nomenclature in light of the disadvantages that the subspecies category carries. It may be that in the future, this disadvantage will be too much to overcome by just a few workers and these populations will best be recognized as different species.

Biogeography

The distribution of *Goniurosaurus kuroiwae* throughout

the Ryukyu Archipelago seems to be rather incomplete. There are large gaps between insular localities within which there are islands with well suited habitat where *G. kuroiwae* is apparently absent (Fig. 8). This absence appears not to be an artifact of collecting because the herpetology of these islands is known quite well [46, 57]. The best example of this is the presence of *G. k. splendens* and *G. k. toyamai* on Tokunoshima and Iheyajima Islands, respectively, and the absence of *G. kuroiwae* from the geographically intermediate Okinoerabujima Island (Fig. 8).

The geological and tectonic history of the Ryukyu Archipelago indicates that the backbone of the Ryukyus was uplifted during the late Miocene as a result of oceanic crust from the Philippine Plate being thrust below the continental crust of Asia [27, 29, 31]. Subsequently, the Ryukyus have had two separate landbridge connections to Taiwan and continental China [23, 24]. The first of these lasted from the late Miocene to the early Pliocene and the second occurred in the early Pleistocene. The majority of the terrestrial reptiles from the Ryukyu Archipelago have their closest relatives occurring in Taiwan and Fukien, the nearest coast on the Chinese continent. Thus, it is assumed here that their ancestors dispersed through the landbridge from the latter regions during the presence of the second landbridge in the early Pleistocene [24, 48, 54]. On the other hand, a few Ryukyu species do not have sister taxa in Taiwan and Fukien and such a relictual distribution pattern is interpreted here as being indicative of a more ancient entry into the Ryukyu Archipelago [23, 24]; perhaps during the first landbridge connection in the late Miocene. The absence of eublepharid geckos from Taiwan and other surrounding regions and the presence of other *Goniurosaurus* from the Gulf of Tonkin (*G. lichtenfelderi*) and southern China (*Goniurosaurus* sp. [14, 15, 33]) may indicate that the ancestral form of *G. kuroiwae* entered the Ryukyus from continental China during the first landbridge formation.

With the submergence of the first landbridge in the middle Pliocene, a large island was formed connecting Kumejima Island of the south to Amamioshima Island of the extreme north [23, 24]. Such a large island would have effectively isolated this ancestral *Goniurosaurus* and presumably promoted the evolution of the ancestor of *G. kuroiwae*. Despite the reunion of this island with Taiwan and continental China during the early Pleistocene, the ancestor of *G. kuroiwae* presumably remained in the Ryukyus probably due to various ecological factors and did not reinvade the continent.

Rising sea levels in the middle Pleistocene resulted in the submergence of the second landbridge. This also began the formation of the contemporary configuration of the Ryukyu Archipelago by creating primary divisions within its central portion. Initially five island groups were formed: Kumejima Island; an island which composed of Tonakijima, Akajima, Tokashikijima, and the other geographically proximate islands; an island composed of Okinawajima, Kourijima, Sesokojima, and Iejima Islands; Iheyajima Island; and Tokunoshima Island [23, 24, 28] (Fig. 8). Unfortunately, there is very little geological data regarding the relative sequence of the isolation of these islands although the biological data presented here (i.e. the phylogenetic relationships) would suggest that it occurred from south to north (Fig. 9).

It is highly probable that all the above islands except Iheyajima and Tokunoshima Islands were re-connected with each other by land bridges during the most recent continental glaciation (ca 15000–18000 yr ago) when the sea level dropped by no less than 120 m [49]. This, however, does not seem to have provided good opportunities for gene flow or range extension for most forest-dwelling reptiles especially on Kumejima Island. The reason is likely due to the very short duration of the connection or the absence of appropriate habitat which would have offered favorable environments on the bridges. Presence of the endemic montane snake, *Opisthotropis kikuzatoi*, on Kumejima [56, 57] and the large genetic divergences between Kumejima, Tokashikijima, and Okinawajima populations of several forest-dwelling species of reptiles revealed by biochemical studies (Ota in prep.), seem to support for this hypothesis. Subsequent rising of the sea level near the end of the Pleistocene would have divided this land mass into the current islands of Kumejima, Tonakijima, Akajima, Tokashikijima, and their surrounding islands, as well as Okinawajima, Sesokojima, Kourijima, and Iejima Islands.

The paleogeographical scenario seems to largely coincide with the evolution of various lineages within *Goniurosaurus kuroiwae* (Fig. 5), although it does not offer any corroborative data as to the chronological sequence in which these lineages evolved. The classification presented above generally reflects the paleogeography of the islands except for the assignment of the Iejima population to *G. k. orientalis*. No evidence suggests that this island was connected to Tonakijima, Akajima, and Tokashikijima Islands to the exclusion of Okinawajima Island [23, 24, 49]. Moreover, similarities in both extant and fossil faunas imply that Iejima Island is historically related to Okinawajima [45]. Thus, it is likely that the apparent similarity of the Iejima population to the Tonakishima, Akajima, and Tokashikijima populations is the result of parallel evolution and not dispersal (*contra* Shimojana [52]).

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kuroiwae from various lacalities, and for the permission to name the subspecies in his honor. For helpful comments on the manuscript we wish to thank R. Etheridge, J. McGuire, B. Hollingsworth, D. Archibald, M. Simpson, and two anonymous reviewers. The work of H. Ota was partially supported by Grants-in-Aid from the Japan Ministry of Education, Science, and Culture (A-63790257, 05740523; to Ota), and the U.S. National Geographic Society Grant (No. 4505-91; to M. Matsui).

Goniurosaurus kuroiwae has been designated as a natural monument of Okinawa Prefecture and the handling of this species is strictly regulated by law. This research was carried out under the permission from the Section of Culture, Okinawa Prefectural Government.

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APPENDIX I

Specimens Examined

All abbreviations follow Leviton *et al.* [32] except those as follows: KUZ-Department of Zoology, Faculty of Sciences, Kyoto University, Japan; LLG-L. Lee Grismer, Department of Biology, San Diego State University, San Diego, CA 92182, USA; and TPN-Satoshi Tanaka, Motobu Senior High School, Tokuchi 377, Motobu, Okinawa 905-02, Japan.

Goniurosaurus kuroiwae kuroiwae: JAPAN-RYUKYU ARCHIPELAGO: OKINAWAJIMA ISLAND; Naha (KUZ 10005–06, TPN 76042508, 76042802, 77041005, 7711060-611, 78011101, 78011401, 78020201, 78031801–05, 78041401–09, 78051601–09, 78060502, 78061501–09, 78061801, 78062501, 78063001, 78070301, 78070401, 78071401–10, 78071701, 78071902, 78072001–02, 78072101, 78072201, 78081401–11, 78081601, 78091601, 78091701–07, 78100601, 78091701–07, 78100601, 78102301–09, 79061001, 79070201, 79070301–02, 79072801, 79082601), Seihua (KUZ 7955, 7957–58, 8002, 8004–05, 8051–53, TPN 6091507–13, 76102111–13, 77040802–05, 77040807–42, 78051701–02, 78052202, 78052701–02, 78052901–04, 78062201–02, 78062401, 7806201–03), Chinen (KUZ 10007), Yakena (TPN 77041701), Oyakebaru (TPN 77121001), Yonaha (TPN 76052401, 76052406, 78032701–03), Yona (TPN 77041401, 77050201–04, 77052101, 77060901, 77081804–12, 77081911–12, 77082102–04, 78042302), Hentona (TPN 78042305–08), Haneji (TPN 79081101–03). KOURIJIMA ISLAND; OPM 424. SESOKOJIMA ISLAND; OPM 369. *Goniurosaurus kuroiwae orientalis*: JAPAN-RYUKYU ARCHIPELAGO: AKAJIMA ISLAND; OPM 341. IEJIMA ISLAND; KUZ 9991. TOKASHIKIJIMA ISLAND; KUZ 7976, OPM 325, NSMT 2523–24, TPN 77101501, 77111701, 77120701–05, 78030101–03, 78052001–03, 78052101–09, 78052201, 78060501, 78061101, 78061401, 78061601, 78071101, 78071201, 78071901, 78072003, 78080501–02, 78080508–10, 78080512–15, 78090202–05, 79082602–03. TONAKIJIMA ISLAND; OPM 489, NSMT 02522. *Goniurosaurus kuroiwae splendens*: JAPAN-RYUKYU ARCHIPELAGO: TOKUNOSHIMA ISLAND; Kedoku (KUZ 8408–11, OPM 10, LLG 1180, 1251–52, NSMT 2514–20, 3211–12, TPN 76102201–04, 77041001–04, 77120901). *Goniurosaurus kuroiwae toyamai*: JAPAN-RYUKYU ARCHIPELAGO: IHEYAJIMA ISLAND; KUZ 9978–83, 9985–88, TPN 77032201, 77070301, 77070401–02. *Goniurosaurus kuroiwae yamashinae*: JAPAN-RYUKYU ARCHIPELAGO: KUMEJIMA ISLAND; KUZ 9989, 9998, 13249, OPM 3, 8, 9, TPN 78050401–02, six uncatalogued specimens. *Eublepharis angramainyu*: CAS 86333, 86337, 86361–62, 86366, 86381, 86383, 86385, 86396–98, 86416, 157129. *Eublepharis harwickii*: AMNH 57593, BM 1927.8.9.1, 1962.23, 1962.38. *Eublepharis macularius*: AMNH 57594, CAS 96212, 96245, 101440–41, 104361–63, 133826, FMNH 161142, LACM 109902–03. LLG 1393–94, 131–38. *Eublepharis turcmenicus*: ZIL 10103, 15380, 19414. *Hemitheconyx caudicinctus*: AMNH 104409, CAS 55114, 154299–302, LLG 2119–96. *Hemitheconyx taylori*: BM 1946.8.26.57–59, 1946.8.26.72, 12.5.372–74. *Holodactylus africanus*: CAS 125431, MCZ 21663, 38693, 53593, 77365–67, 77369–70, 96928, 160707. *Holodactylus cornii*: BM 1931.7.20.269.